

# DRAGLINE-FOLLOWING BY MALE LYCOSID SPIDERS<sup>1</sup>

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Wolf spiders stalk or ambush their prey rather than build prey-capture webs. Production of silk by lycosids is important during aerial dispersal via ballooning (Richter, 1970b) and, in some, during post-immobilization wrapping of prey (Rovner and Knost, 1974), and construction of egg sacs or sperm webs (Richter, 1970a). During locomotion both sexes lay down silk draglines that are generally assumed to have a stabilizing or security function (Richter and Van der Krann, 1970). In addition, female draglines induce courtship behavior in male conspecifics and, in some species, males are reported to have followed a female trail, but no systematic analyses of the dragline-following behavior have been attempted (Bristowe and Locket, 1926; Engelhardt, 1964; Kaston, 1936).

The present study is concerned with the trail-following behavior of male *Lycosa rabida* and *L. punctulata*. Specific areas of investigation include determination of the use of various appendages during following, analysis of cues involved in initiating and maintaining trail-following, and an interspecific comparison of trail-following behavior.

## METHODS

Penultimate and young adult instars of *L. rabida* and *L. punctulata* were collected near Amesville, Athens County, Ohio, USA, during 1974 and 1976. *L. rabida* were collected late June through July while *L. punctulata* were collected mid- to late September.

Animals were housed separately in 13 × 7 × 6.5 cm plastic cages painted on two sides to afford visual isolation between animals in adjacent cages. A paper substratum in each cage collected silk used in some experiments and facilitated periodic cleaning of the cages. Water was provided ad libitum via a cotton-stoppered vial, and two *Tenebrio* sp. larvae were provided per week as food. Cages

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containing males were located on shelves along one wall of the laboratory that received indirect sunlight. Laboratory humidity was not controlled (range 36–56% RH) and temperature ranged from 23–28°C. Cages containing females were placed in a controlled environmental chamber (Frease model 818) at 15°C night and 20°C day and 53–56% RH, with a photoperiod approximating natural conditions. The lower temperatures were necessary to retard female development and to delay onset of eggsac production, which even occurs eventually in unmated females, making them useless for further experimentation. Females were removed from the environmental chamber and allowed sufficient time to warm to room temperature before experimental use.

In order to lay draglines along predetermined trails spiders were anesthetized with CO<sub>2</sub>. A thread leash, secured to a hemostat, was tied around the cephalothorax of each spider between the second and third pairs of legs. Upon recovery, the spider was led along a path such that the dragline was laid either directly on the substratum to form “ground lines” or suspended above the substratum by being laid across horizontally placed glass rods to form “aerial lines” (Fig. 1). Lines connecting parts of an artificial plant made of wood dowels were also called “aerial lines.” Male draglines or imitation draglines (nylon thread or human hair) were laid in either a continuous or discontinuous manner with the female trail during some experiments.

The test trail was then surrounded by glass walls to provide an arena (54 × 64 cm), the position of which was rotated in a random manner between experimental runs. The position, length, and direction of the dragline, including attachment disks (produced by the spider to fix the dragline to a substratum) were recorded on a diagram of the completed path.

Test males were of two physiological conditions: (1) unprimed males, which had not encountered female silk for the previous 72 hr and (2) primed males, which were induced to court in response to substratum silk from a female cage, and then tested 1 hr later for dragline-following behavior. Experimental trials began when a male released into the arena contacted and explored a female line with his palps. Trials lasted for 5 min, during which time data were recorded in shorthand notation from a distance of 0.5–1.0 m from the experimental males. To test the response of males to various types of silk, males were released into cages containing either lepi-

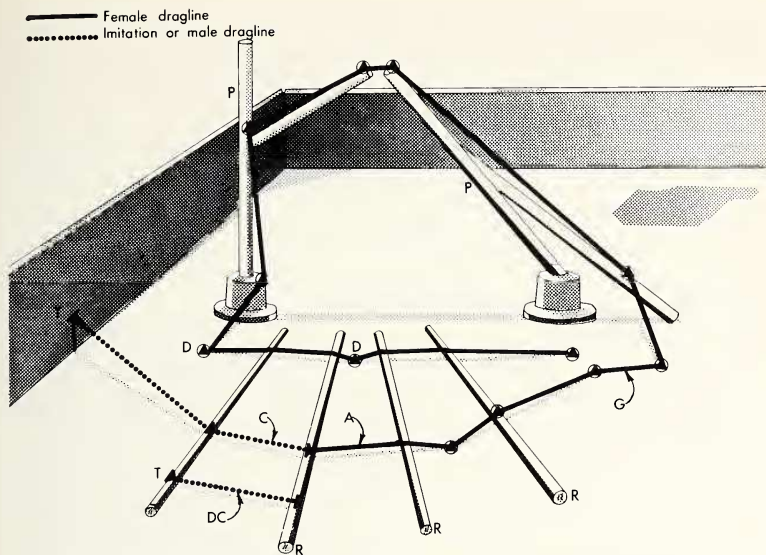


Figure 1. Diagrammatic summary of a typical trail including attachment disks (D) and female aerial lines (A). Female ground lines (G) and imitation draglines are laid contiguously (C) and discontinuously (DC) with the female dragline. Small strips of masking tape (T) attach imitation dragline to the wall of the arena and to 5-mm diameter glass rods (R). Glass rods were usually parallel and 9–11 cm apart. When artificial “plants” (P) were incorporated into the experiment, female trails up to 236 cm in length were constructed.

dopteran silk or conspecific male or female silk. Male *L. punctulata* were also exposed to female *L. rabida* silk. Clean cage cards were used as controls. A positive response by males to the silk consisted of exploring the silk and initiating courtship behavior within 5 min.

Statistical analyses of data were performed according to the methods of Conover (1971) and Sokal and Rohlf (1969). All means are accompanied by their standard errors.

## RESULTS

### COMPARISONS OF YEARLY SAMPLES

No difference was found in trail-following behavior between 1974 and 1976. Unprimed male *L. rabida* showed no difference in frequency of following-behavior ( $\chi^2 = 0.0$ ,  $df = 1$ ,  $P > .50$ ) and in

total distance followed during the 5-min test period (Mann-Whitney test,  $T = 173, P > .80$ ). Primed male *L. rabida* showed no difference in frequency of following ( $\chi^2 = .504, df = 1, P > .70$ ) or in total distance followed (Mann-Whitney test,  $T = 229.5, P > .56$ ). Male *L. punctulata* showed no difference in the frequency of following ( $\chi^2 = 2.5, df = 1, P > .90$ ) or in total distance followed (Mann-Whitney test,  $T = 235.5, P > .84$ ). Therefore, data for the two years were pooled for analysis.

#### DESCRIPTION OF DRAGLINE-FOLLOWING

Males of both species followed conspecific female lines. Although high speed (36–180 fps) cinematographic analysis indicates that there are slight differences in the use of appendages during dragline-following (Tietjen, unpublished data), the two species exhibit many similarities. Upon contacting the silk line for the first time, males tend to examine it with alternating movements of the palps such that the dorsal surface of the palp contacts the line and moves anteriorly along it. Such behavior is soon terminated if the line is a male's or is an imitation. Dragline-following results if the line is that of a female conspecific. Males usually wander to the edge of the arena and walk around the periphery if chemo- and mechano-exploratory behavior is terminated.

In both species, dragline-following is characterized by the male straddling the silk so that it passes medially beneath him. Although the first pair of legs may occasionally pluck at the line, the palps are the most important appendages used. The palps are alternately moved forward and back, making contact with the silk on their medial surface rather than on the dorsal surface, which is used during the initial contact with the line. Experiments conducted under red light (Kodak safelight Filter No. 1) and with blinded animals indicated that vision is not necessary for dragline-following. Males may accompany their dragline-following behavior with elements of courtship or, more typically, interrupt dragline-following with separate bouts of courtship behavior.

#### DRAGLINE-FOLLOWING BY *LYCOSA RABIDA*

Both primed and unprimed male *L. rabida* followed female aerial draglines. Unprimed males exhibited a lower incidence of dragline-following, with 84.6% of primed and 65.2% of unprimed following ( $\chi^2 = 5.83, df = 1, P < .025$ ). Comparing only those males that

Table I: Performance of Male *Lycosa rabida* and Male *L. punctulata* During Dragline-Following of Conspecific Male, Female, and Imitation Silk.

	<i>L. rabida</i>		<i>L. punctulata</i>
	Primed	Unprimed	Pooled
Number of males tested	52	69	57
number following	44	45	40
number not following	8	24	17
Distance (cm)			
$\bar{Y}$ total distance	23.1 ± 2.3	26.7 ± .2	56.9 ± 8.7
$\bar{Y}$ polarity	+ 7.9 ± 3.3	- 6.5 ± 4.2	+ 5.3 ± 2.4
Courtship			
Frequency	27.2%	26.6%	12.5%
$\bar{Y}$ latency (min)	1.4 ± .4	1.1 ± .3	1.4 ± .8
Imitation and male draglines			
number followed	7	4	0
number not followed	6	12	16
Ground lines			
number followed	0	0	13
number not followed	18	9	4

followed draglines, no significant difference was found in the total distance followed between primed and unprimed animals (Mann-Whitney test,  $T = 1069.5$ ,  $P > .72$ ). No males of either group followed *ground* lines, although they would usually examine such lines with their palps (Table I).

None of the male *L. rabida* followed isolated imitation draglines; and chemoexploratory behavior to such lines was exhibited only five times. Males in the process of following a female line would occasionally follow imitation and male draglines laid contiguously with the female trail (Table I). Once, a male following a female line continued on and followed the entire length of a human hair that constituted an 8.5 cm interruption in the female trail, losing no momentum in his following behavior. Male draglines were followed four times, human hairs were followed six times and nylon thread was followed once.

The polarity of each male's trail was calculated as the difference between total distance traveled in the same direction as the female

trail was laid and total distance traveled in the opposite direction. Primed males exhibited a positive polarity by following the correct direction more often than the incorrect direction ( $\chi^2 = 7.36$ ,  $df = 1$ ,  $P < .01$ ), and by traveling further in the correct direction along the female trail (Wilcoxon test,  $T = 252.5$ ,  $P < .01$ ). Unprimed males did not show a directional preference ( $\chi^2 = 0.0$ ,  $df = 1$ ,  $P > .50$ ; Wilcoxon test,  $T = 525$ ,  $P > .64$ ; Table I).

Primed and unprimed male *L. rabida* showed no difference in the frequency of courtship during dragline-following ( $\chi^2 = .613$ ,  $df = 1$ ,  $P > .50$ ) or in the elapsed time during a test before courtship was observed (= courtship latency) (Mann-Whitney test,  $T = 70.0$ ,  $P > .54$ ; Table I). Primed males that courted showed no correlation between total distance of dragline followed and courtship latency (Spearman's rho,  $\rho = + .026$ ,  $P > .53$ ). Unprimed males courting early in the test showed decreased total dragline-following (Spearman's rho,  $\rho = + .692$ ,  $P < .01$ ). Comparing primed and unprimed males that both courted and followed draglines, no difference was found in the total amount of dragline-following (Mann-Whitney test,  $T = 747.0$ ,  $P > .65$ ).

#### DRAGLINE-FOLLOWING IN *LYCOSA PUNCTULATA*

*L. punctulata* was a more difficult species to study experimentally than *L. rabida*. Females often would not lay the required lines and both sexes tended to break the lines by catching a claw on them, and the males by running through the lines.

In 1974, 9 of 10 males in each group exhibited dragline-following. The total distance followed for primed ( $\bar{Y} = 63.1 \pm 20.7$  cm) and unprimed ( $\bar{Y} = 63.1 \pm 17.5$  cm) males did not differ significantly between the two groups (Mann-Whitney test,  $T = 47.5$ ,  $P > .57$ ). Incidence of courtship did not differ between the two groups with primed males courting during one and unprimed males courting during three of the trials ( $\chi^2 = 1.25$ ,  $df = 1$ ,  $P > .70$ ). Data for the two groups were pooled for further analysis.

In 1976 only unprimed males were used. During 34 trials 23 males followed a mean total distance of  $52.4 \pm 11.3$  cm. No differences were found between pooled 1974 data and the 1976 (all unprimed) data for incidence of following ( $\chi^2 = 3.41$ ,  $df = 1$ ,  $P > .05$ ), or for distance followed (Mann-Whitney test,  $T = 235.5$ ,  $P > .77$ ). Unprimed males in 1976 exhibited courtship three times during dragline-following; no difference in courtship frequency was

found between the pooled 1974 data and those for 1976 males ( $\chi^2 = 0.34$ ,  $df = 1$ ,  $P > .70$ ). In order to have a larger data base the data were pooled for both years.

Unlike male *L. rabida*, male *L. punctulata* initiated dragline-following at ground lines and appeared to use their palps in a manner similar to chemoexploratory behavior. Male *L. punctulata* rarely examined isolated male lines or imitation lines; of 16 that did palpate these lines, none followed them (Table I). Males exhibited a positive polarity ( $\chi^2 = 4.33$ ,  $df = 1$ ,  $P < .05$ ), and traveled a greater distance in the correct direction along the female trail (Wilcoxon test,  $T = 255.5$ ,  $P < .03$ ).

Males that courted during dragline-following showed no correlation between courtship latency and distance followed (Pearson's  $r$ ,  $r = + .700$ ,  $P > .90$ ). No difference in distance followed was found between males that courted during dragline-following and those that did not (Mann-Whitney test,  $T = 93.0$ ,  $P > .58$ ). Courtship latency of males placed on a female substratum was affected after dragline-following; those which had recently followed a dragline exhibited a mean courtship latency of  $0.66 \pm .29$  min ( $N = 23$ ) compared with  $2.30 \pm 0.25$  min ( $N = 20$ ) for those which had not (Mann-Whitney test,  $T = 52.0$ ,  $P < .0001$ ).

#### COURTSHIP RESPONSES TO VARIOUS TYPES OF SILK

Male *L. rabida* courted in response to silk in a female cage in 50% of the trials. Courtship latency in response to female silk was  $2.30 \pm .25$  min. The incidence of courtship in response to female silk differed from the courtship frequency in response to a clean cage, lepidopteran silk and male *L. rabida* silk ( $\chi^2 = 33.99$ ,  $df = 3$ ,  $P < .001$ ). The incidence of courtship did not differ among the latter three conditions ( $\chi^2 = 2.05$ ,  $df = 2$ ,  $P > .70$ ). (Table II).

Male *L. punctulata* courted in response to female conspecific silk in 61.1% of the trials and exhibited a mean courtship latency of  $2.55$  min  $\pm .44$  min. The incidence of courtship in response to female conspecific silk, female *L. rabida* silk, lepidopteran silk, a clean cage and male *L. punctulata* silk differed significantly ( $\chi^2 = 35.93$ ,  $df = 4$ ,  $P < .001$ ), while courtship frequency did not differ among the latter four test conditions ( $\chi^2 = 2.10$ ,  $df = 3$ ,  $P > .50$ ).

To simulate the effects of dew under natural conditions, silk trails of females of both species were sprayed with a fine mist of distilled water and were air dried (= washed lines). Draglines so

Table II. Courtship Responses to Various Types of Silk by Male *Lycosa rabida* and Male *L. punctulata*.

	Experimental Silks				
	Clean cage	Female con-specific	Male con-specific	Female hetero-specific	lepidopteran
<i>L. rabida</i>					
number tested	20	40	20	0	20
number courting	1	20	0	—	0
number not courting	19	20	20	—	20
$\bar{Y}$ courtship latency (min)	1.27	2.30 ± .2	—	—	—
<i>L. punctulata</i>					
number tested	20	18	20	20	20
number courting	2	11	1	0	1
number not courting	18	7	19	20	19
$\bar{Y}$ courtship latency (min)	4.06 ± .7	2.55 ± .7	4.93	—	4.57

treated lost elasticity and drooped between the supporting glass rods. Both unprimed male *L. rabida* ( $N = 10$ ) and unprimed male *L. punctulata* ( $N = 10$ ) exhibited short bouts of chemoexploratory behavior at washed lines, but neither species exhibited courtship or trail-following behavior during the 5-min trials.

#### DISCUSSION

Trail-following has been observed in a variety of arthropods. Terrestrial chemical trails are often employed by eusocial insects, but such trails are detected by the receiver as a rapidly decaying vapor cloud above the substratum and provide no directional information (Wilson, 1971). Lepidopteran larvae (*Malacosoma*, *Hypnomena* and *Thaumetopoea*) have been observed to follow silk trails from their nest to a food source; but tactile information provided by the silk is unimportant, and the pheromone decays within a few minutes (Fitzgerald, 1976; Wigglesworth, 1966). Wolf spider trails differ from the above examples in function (mating vs. food), in the use of a contact rather than an olfactory pheromone, and in the presence of an inherent polarity. Silk lines in the



laboratory up to 4 days old will elicit following-behavior in male *L. rabida* and male *L. punctulata*; and a cage substratum with female silk elicits courtship behavior for over a month (Tietjen, unpub. data), indicating that the spider pheromone does not decay over a relatively long period of time.

Female lycosid spiders exhibit low motility during the breeding season and adopt a "sit and wait" reproductive strategy; the highly active males seek out the females (Hallander, 1967a, 1967b; Hallander, 1972; Muma, 1973; Richter, et al., 1971). Mathematical modeling of females laying no silk trails and silk trails of various lengths indicates that the presence of silk effectively increases the size of the female target as perceived by the searching male (Tietjen, unpub. data). Thus, the ability of male *L. rabida* and *L. punctulata* to follow conspecific female draglines to the source increases the reproductive success of these males over spiders that depend on chance encounters in a heterogeneous environment. Female silk also alerts the male to the presence of a female conspecific and, as shown in *L. punctulata*, decreases the courtship latency. The latter two functions effectively reduce the likelihood of intraspecific cannibalism (Platnick, 1971).

Contact sex pheromones associated with the female dragline are known to induce courtship in conspecific male spiders (Dijkstra, 1970; Dondale and Hegdekar, 1973; Hegdekar and Dondale, 1969). Results from the present study support the hypothesis that a pheromone associated with the female dragline elicits courtship in receptive males, i.e., these behaviors are not dependent exclusively upon tactile information provided by the silk. Both *L. rabida* and *L. punctulata* are found with a variety of other spider species. Dependence on a pheromone to elicit sexual behavior in males would reduce the chances of males following draglines of other species and thereby adversely affecting the time budget allocated for reproductive purposes.

The propensity of male *L. rabida* not to follow ground lines which cannot be plucked by the palps (thereby providing little tactile input) and their occasional following of imitation draglines, which provide no chemical cues, indicate that the pheromone is responsible only for initiating the following behavior in males. Once a male is following a dragline, tactile cues appear to be adequate. Males are expected, however, to occasionally sample the trail for female pheromone, as only 38% of male and imitation

dragline contacts during female dragline-following resulted in following by males, and most imitation draglines were not followed the entire length.

Male *L. punctulata* followed ground lines, but did not follow male and imitation draglines. This species appears to depend upon the female pheromone for initiating and for maintaining dragline-following. Apparently, male *L. punctulata* are either more sensitive to tactile input provided by ground lines, or more sensitive to pheromonal cues than male *L. rabida*, or both.

The differential sensitivity to tactile and chemical cues exhibited by the two species may be related to microhabitat preferences. *L. punctulata* is found in the lower levels of the herbaceous stratum (Eason and Whitcomb, 1965) in which one expects a greater diversity and density of spiders (Whitcomb, Exline and Hite, 1963) and consequently more draglines. Many lycosids of similar or larger size are found within this microhabitat of which male *L. punctulata* could be potential prey, including *L. helluo* and *L. carolinensis*. Continuous sampling for female pheromone during dragline following reduces the likelihood that males will follow another species' trail in a high silk density microhabitat. In addition, due to the greater foliage density at this level, many draglines could be expected to be laid directly on a substratum. A greater sensitivity to tactile and/or chemical cues could allow male *L. punctulata* to follow such ground lines.

*L. rabida*, on the other hand, is found high in the herbaceous stratum (Eason and Whitcomb, 1965; Kuenzler, 1958) and is associated with lower interspecific silk densities derived mainly from smaller species such as salticids and oxyopids. Foliage density is less, and a greater volume of open space is found at this level. Fewer female silk trails would be expected to be found directly on this substratum. Under these conditions the sensitivity to tactile and/or chemical cues exhibited by *L. punctulata* would not be required for efficient dragline-following by male *L. rabida*.

Silk lines are destroyed mechanically in the field by wind and the activities of animals. Moisture resulting from rain and early morning dew inactivates the female pheromone found on unbroken lines (Dondale and Hegdeker, 1973; Hegdeker and Dondale, 1969). All of these effects reduce the likelihood that males will follow draglines laid the previous day.

Male *L. punctulata* and primed male *L. rabida* may be able to extract directional information from the female dragline, though it is unlikely that a pheromone concentration gradient could provide the directional information since the pheromone remains active over long periods of time. Examination of female *L. rabida* silk under a light microscope (450 $\times$ ) as well as scanning electron microscope inspection of female *L. punctulata* silk (1000 $\times$ ) indicate no evidence of structural features on the dragline which could provide directional information to males.

Spiders are able to detect slight changes in web tension through vibration receptors during prey capture, web building, and courtship (Robinson, 1969; Walcott, 1969; Witt, 1975). Such variations in tension, related to the direction in which the dragline was laid, could provide directional information to dragline-following males. If present, the tension differential may be related to the structure of the attachment disk by which the silk is fixed to a substratum. As the dragline enters the attachment disk it is tightly wound, whereas the silk leaving the attachment disk is composed of single threads which later join and wind to form the dragline. Single silk threads leaving an attachment disk would be expected to damp transients produced along the line more readily than a complete dragline entering an attachment disk. If this were the case, dragline-following toward the pole with the higher resonant frequency would constitute movement in the direction the silk was laid (Tietjen, unpub. data). Such a system would require that males immobilize a portion of the dragline, perhaps with a palp, while plucking on either side of the fixed portion. Male spiders encountering a female line often wipe the dorsal surface of each palp alternately over the silk and often pluck at the silk with the first legs as they swivel their bodies along a short length of the trail. This behavior may represent both a sampling for female pheromone and a testing for differential mechanical properties of the line related to the direction in which it was laid.

Unprimed male *L. rabida* did not exhibit a polarity in dragline-following, but a positive correlation between courtship latency and total distance followed was observed. The above correlation indicates that unprimed males probably have a lower threshold for chemical cues than do primed males. If unprimed males are attending more to chemical cues, they would be less likely to follow

a dragline in a preferential direction if directional cues were dependent on the mechanical properties of the line.

#### SUMMARY

The dragline-following behavior of male wolf spiders was observed in response to male, female and imitation draglines. Male *L. rabida* followed female draglines suspended above the substratum but not those laid directly on the substratum. These males followed male silk and imitation lines if laid contiguously with female draglines, suggesting that they depend on tactile cues during dragline-following. On the other hand, male *L. punctulata* followed both aerial lines and ground lines laid by females but did not follow imitation or male lines. This suggests that male *L. punctulata* are more sensitive to tactile and/or chemical cues than are male *L. rabida*. Microhabitat preferences of the two species may explain the above differences. Data also suggest that males of both species are able to extract directional information from the dragline, perhaps by tensional cues.

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